PRIMARY RESEARCH ARTICLE

Alpine glacial relict species losing out to climate change: The case of the fragmented mountain hare population (*Lepus timidus*) in the Alps

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Abstract

Alpine and Arctic species are considered to be particularly vulnerable to climate change, which is expected to cause habitat loss, fragmentation and—ultimately—extinction of cold-adapted species. However, the impact of climate change on glacial relict populations is not well understood, and specific recommendations for adaptive conservation management are lacking. We focused on the mountain hare (*Lepus timidus*) as a model species and modelled species distribution in combination with patch and landscape-based connectivity metrics. They were derived from graph-theory models to quantify changes in species distribution and to estimate the current and future importance of habitat patches for overall population connectivity. Models were calibrated based on 1,046 locations of species presence distributed across three biogeographic regions in the Swiss Alps and extrapolated according to two IPCC scenarios of climate change (RCP 4.5 & 8.5), each represented by three downscaled global climate models. The models predicted an average habitat loss of 35% (22%–55%) by 2100, mainly due to an increase in temperature during the reproductive season. An increase in habitat fragmentation was reflected in a 43% decrease in patch size, a 17% increase in the number of habitat patches and a 34% increase in inter-patch distance. However, the predicted changes in habitat availability and connectivity varied considerably between biogeographic regions: Whereas the greatest habitat losses with an increase in inter-patch distance were predicted at the southern and northern edges of the species' Alpine distribution, the greatest increase in patch number and decrease in patch size is expected in the central Swiss Alps. Finally, both the number of isolated habitat patches and the number of patches crucial for maintaining the habitat network increased under the different variants of climate change. Focusing conservation action on the central Swiss Alps may help mitigate the predicted effects of climate change on population connectivity.

KEYWORDS
biogeography, connectivity, conservation priorities, habitat fragmentation, species distribution modelling, Swiss Alps

1 | INTRODUCTION

Climate change is leading to higher temperatures, changing precipitation patterns and more frequent extreme weather events (IPCC, 2014). These changes are affecting species' distributions, phenology and physiology worldwide (Hughes, 2000; Menzel et al., 2006; Parmesan, 2006; Parmesan & Yohe, 2003; Root et al., 2003; Walther et al., 2002). Alpine and Arctic species have been identified as being especially vulnerable to global warming (Beever, Ray, Wilkening, Brussard, & Mote, 2011; Hughes, 2000; Jackson, Gergel, & Martin, 2015; Moritz et al., 2008; Parmesan, 2006; Thuiller, Lavorel, & Araujo, 2005; Wilkening, Ray, Beever, & Brussard, 2011), partly because warming may occur more rapidly at higher elevations (Pepin et al., 2015). Moreover, these species have evolved specific adaptations to cold environments and often lack the capacity to adapt quickly enough to climatic changes (Hof, Levinsky, Araujo, & Rahbek, 2011; Mace & Purvis, 2008; Parmesan, 2006) or may already be living near their physiological limits (Furrer et al., 2016; Hoffmann & Sgro, 2011).

One way of adapting to climate change is to shift to colder environments in higher latitude and altitude (Parmesan & Yohe, 2003). However, for mountain species this further exacerbates the extinction risk as the more they progress upwards on mountain slopes, the smaller is the area and the narrower the availability of a given habitat due to the intrinsic conic shape of mountains (Elsen & Tingley, 2015). Here, increasing temperatures will not only lead to habitat loss but concurrently increase habitat fragmentation, that is, the distances between mountain-top habitats (Fahrig, 2003). This may result in reduced gene flow among populations, inbreeding within isolated populations, a further reduction in the population's ability to adapt to the changing environment (Reed & Frankham, 2003; Rudnick et al., 2012; Van Strien et al., 2014), and ultimately extinction (Calkins, Beever, Boykin, Frey, & Andersen, 2012; Erb, Ray, & Guralnick, 2011; Hanski, 1998; Moritz et al., 2008; Thomas et al., 2004). Understanding the drivers and spatial response patterns of threatened mountain biodiversity to climate change has therefore become crucial for developing appropriate conservation measures.

Species distribution models (SDMs), which simulate climate change effects on habitat availability and configuration, are increasingly being used to support decision-making in conservation (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Guisan et al., 2013; Porfirio et al., 2014). SDMs extrapolate current species-habitat associations to future environmental conditions so that potential changes in species distributions can be forecast. This allows to develop and implement targeted conservation measures for the benefit of the focal species (Bollmann & Braunisch, 2016; Braunisch et al., 2014; Hope et al., 2015).

Changes in the size and distribution of habitat patches over time affect structural, and often also functional, habitat connectivity. Predicting these changes and identifying key areas for maintaining or restoring habitat networks so as to allow species to track suitable climate conditions is therefore of major importance (e.g. Elith &

Leathwick, 2009). Functional responses to habitat connectivity are inherently species-specific. Modelling connectivity therefore requires information about species' movement in relation to the landscape matrix (Fahrig, 2003; Fischer & Lindenmayer, 2007; Hanski, 1998; Nicol et al., 2016; Pascual-Hortal & Saura, 2006; Rudnick et al., 2012). Graph modelling approaches are an increasingly popular method of analysing habitat networks (Baranyi, Saura, Podani, & Jordan, 2011). These models consider habitat patches as nodes in a landscape matrix connected by links defined by the species' movement ability and have the advantage that they can also be applied to situations where the habitat patches and dispersal distances are known, but the species-specific landscape permeability is not. The models produce a range of connectivity metrics that allow to quantify the overall habitat connectivity for a given species in a given landscape as well as the contribution of single habitat patches to the network (Galpern, Manseau, & Fall, 2011; Saura & Torne, 2009).

The mountain hare (*Lepus timidus*) is considered a suitable model species to analyse climate-induced habitat fragmentation in mountain ecosystems (Hackländer, Ferrand, & Alves, 2008) because it is a genuine Arctic species in its Alpine range where it lives in isolated glacial relict populations with high site fidelity at high elevations (Bisi et al., 2011; Rehnus, 2013; Schai-Braun & Hackländer, 2016; Thulin, 2003; Thulin & Flux, 2003). Mountain hare populations seem, however, decreasing in the Alps slowly which led to increasingly restrictive hunting regulations in some regions. Such restrictions have been introduced in, for example, Bavaria and Baden-Württemberg in Germany (Adrian, 2015), Salzburg in Austria (Environment Agency Austria, 2015) and Cantons Berne, Lucerne and Fribourg in Switzerland (Rehnus, 2013). The species is classified as "near-threatened" in the Red Lists of France (The National Red List project, 2015) and Carinthia in Austria (Gutleb, Komposch, & Spitzenberger, 1999). Understanding how climate change will probably influence the spatial distribution and connectivity of mountain hare habitats should therefore elucidate general patterns of habitat changes, which may also affect other Alpine glacial relict species with similar habitat requirements, such as Black grouse (*Tetrao tetrix*) or Rock Ptarmigan (*Lagopus mutus*) (Geary, Fielding, & Marsden, 2013; Pernollet, Körner-Nievergelt, & Jenni, 2015; Schweiger, Nopp-Mayr, & Zohmann, 2012; Signorell et al., 2010).

In this study, we used high-resolution climate, topographic and land-cover data to predict the potential effects of climate change on the distribution and habitat connectivity of the mountain hare in the Swiss Alps under different scenarios of climate change. We hypothesized climate change would result in habitat loss and increasing habitat fragmentation, and that this would be reflected in an increasing number of habitat patches, decreasing patch sizes and an increasing patch isolation. In addition to testing these hypotheses, we also wanted to identify patches that are especially crucial for maintaining an interconnected habitat network under future climate conditions as priority regions for targeted conservation action.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area comprises three biogeographic regions in the Swiss Alps (Figure 1), the Northern, Central and Southern Alps (Gonseth, Wohlgemuth, Sansonnens, & Buttler, 2001), which incorporate the entirety of the mountain hare range in Switzerland. Thus, we were able to consider the species' complete ecological range of topographic, vegetation and climatic conditions, in addition to spatial variance in population densities (Rehnus, Braunisch, Hackländer, Jost, & Bollmann, 2016; Rehnus, Marconi, Hackländer, & Filli, 2013). The habitat in the Swiss Alps is mainly natural or semi-natural. Unproductive areas dominate (36%, 24% of which is rock), followed by forested areas (31%), agricultural areas (30%) and residential areas (3%; Bundesamt für Statistik, 1997).

2.1.1 | The Northern Swiss Alps

The Northern Swiss Alps are characterized by an oceanic climate with dominant winds from the North and the West. Precipitation exceeds 1,200 mm/year at 1,000 m a.s.l. (Ott, Frehner, Frey, & Lüscher, 1997). Temperatures are between of those of the Central and Southern Swiss Alps, with mean January temperatures of −2°C and July temperatures of 15°C. Sunshine duration as measured at Engelberg (1,036 m a.s.l.) is rather low, with 1,350 sun hours per year and slight daily and seasonal variations (Federal Office of Meteorology and Climatology, 2016). Spruce (*Picea abies*) dominates the forests in the subalpine zone and co-occurs with fir (*Abies alba*) at lower elevations (Ott et al., 1997).

2.1.2 | The Central Swiss Alps

The Central Swiss Alps are influenced by a continental climate. The valleys are largely protected from oceanic and insubric (mild and wet) influences by the Alpine massif. Precipitation ranges between 600 and 900 mm/year at 1,000 m a.s.l. (Ott et al., 1997). Sunshine duration in this region is high (1,733 sun hours per year), and daily and seasonal temperatures vary greatly with mean January temperatures of −9°C and July temperatures of 12°C (Samedan 1,709 m a.s.l.; Federal Office of Meteorology and Climatology, 2016). Subalpine forests are dominated by spruce and larch (*Larix decidua*), with Swiss stone pine (*Pinus cembra*) taking over at higher elevations. Swiss stone pine co-occurs with mountain pine (*Pinus mugo*) along the upper timber line and/or in areas influenced by avalanches, whereas Scotch pine (*Pinus sylvestris*) occurs at lower elevations (Ott et al., 1997).

2.1.3 | The Southern Swiss Alps

The Southern Swiss Alps are characterized by a mild climate, with winds from the South and the West and high precipitation throughout the year. The average annual precipitation at 1,000 m a.s.l. is >2,000 mm/year (Ott et al., 1997). Temperatures are warm with mean January temperatures of 1°C and July temperatures of 19°C, and sunshine duration is moderate (1,418 sun hours per year; Acquarossa 575 m a.s.l.; Federal Office of Meteorology and Climatology, 2016). In the subalpine zone, larch and Swiss stone pine are the predominant tree species, with spruce and fir occurring at lower elevations (Ott et al., 1997).

2.2 | Species data

We compiled mountain hare presence data covering a 24-year period from 1990 to 2013 from different sources to ensure a representative distribution of mountain hares across the study area. The informal observations stored in the Swiss faunistic database CSCF (Centre Suisse de Cartographie de la Faune CSCF, 2015) served as a key source. In areas where CSCF data were sparse or missing, we
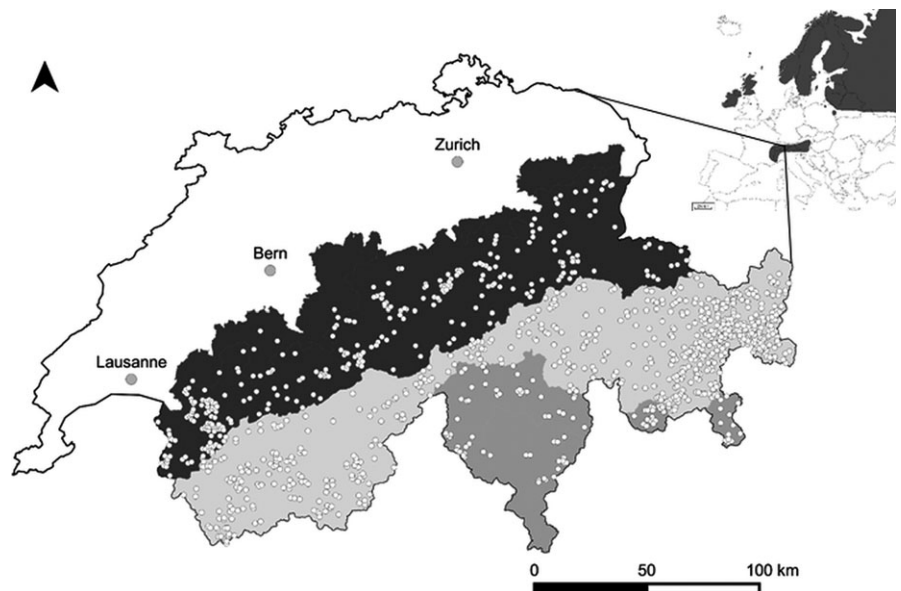

FIGURE 1 Distribution of mountain hare presence data (white dots, N = 1,046) in the Swiss Alps (Black: Northern Swiss Alps; light grey: Central Swiss Alps; dark grey: Southern Swiss Alps; Gonseth et al., 2001; adapted). Top right: The distribution of mountain hares in Europe according to Thulin (2003)

collected complementary presence data (telemetry and monitoring data, hunting bag records, observations, presence of faeces) from research projects (Gamboni, 1997; Rehnus & Bollmann, 2016; Rehnus, Palme, Filli, & Hackländer, 2010; Rehnus, Wehrle, & Palme, 2014; Rehnus et al., 2013, 2016; Zachos, Ben Slimen, Hackländer, Giacometti, & Suchentrunk, 2010), and the long-term observations of the park rangers in the Swiss National Park (Swiss National Park, unpublished). We also compiled records of hunting bags and observations with exact information on the location where an animal had been shot or seen. Only locations with a minimum precision of one hectare were considered ($N = 3,338$). As most data were collected with unknown sampling intensity, we used spatial filtering to minimize the sampling bias and to reduce spatial autocorrelation (Fourcade, Engler, Rödder, & Secondi, 2014; Kramer-Schadt et al., 2013; Phillips et al., 2009). We randomly selected one location within a 400-m radius (i.e. 50.3 ha), which corresponds to roughly the average annual home range of mountain hares in the Alps (MCP95%: 57.5 ha, Nodari, 2006), resulting in the 1,046 presence locations included in the analysis (Figure 1).

2.3 | Environmental variables

The environmental predictors we considered were topography, land cover and climate. We focused on variables that had been identified as relevant to the mountain hare in previous leporid studies (Table 1). While climate variables were allowed to change over time, land-cover variables were held constant for future projections because no reliable projections on land-cover changes were available.

2.3.1 | Topography

Topographical variables, including slope, topographic exposure, distance to the summit and relief roughness, were derived from a digital elevation model (DEM) with a 25-m resolution (Zimmermann & Kienast, 1999; Table 1). The topographic exposure index (Topex) describes a point's position relative to the surrounding terrain by summarizing the angles to the ground measured within a fixed distance of 150 m (Topex 150) for each of the eight cardinal directions. Positive values indicate exposed sites such as hilltops or ridges, whereas negative values represent depressions. Additionally, we used the Topex 1000 (i.e. 1,000-m fixed distance) to determine "summits," which were defined as any exposed site with a Topex 1000 value ≥ 150. Based on this, the distance of each presence point in the study area to the next summit was assessed. Relief roughness was calculated using the topographic ruggedness index developed by Riley, Degloria, and Elliot (1999), which expresses the sum of the change in elevation between a grid cell and its eight neighbouring grid cells. Elevation *per se* was not included in the models because it was highly correlated with climatic conditions and would therefore have blurred the relative importance of climatic variables.

2.3.2 | Land cover

Land-cover variables included shrub cover of bushes, forests, moor, glaciers, rocks and scree, as well as the distance to outer forest edges, water bodies (lakes, rivers and creeks), roads, and anthropized areas (buildings or settlements). These variables were derived from the Vector 25 dataset (Federal Office of Topography, 2015). Land-cover values for meadows, pasture, alpine grassland, other grasslands, dwarf shrubs and herbaceous vegetation were obtained from the area statistics of Switzerland with a pixel size of 100 m (Federal Statistical Office, 1997). These categories were merged to a single variable "Alpine grassland."

2.3.3 | Climate

We used 10 climate variables which are known to influence the distribution of the mountain hare in the Alps (Table 1): length of the growing season, mean diurnal temperature range, precipitation seasonality, amount of precipitation in winter, solar radiation during both summer and winter, as well as mean temperature, precipitation, number of cold days (mean temperature $\leq 5°C$) and number of warm days (mean temperature $\geq 10°C$) during the reproductive season. "Winter" refers to the period from December to February; "summer" to the period from June to August. The "reproductive season" is the period from April to August, corresponding to the reproduction time of the mountain hare in the Alps (Rehnus, 2013).

"Current climate" refers to the period from 1990 to 2013, corresponding to the sampling period of the species data (24 years). To generate area-wide climate information, we used Daymet (Thornton, Running, & White, 1997), an interpolation software designed to produce gridded estimates of daily weather parameters from local weather station data and a DEM. As input, we used daily temperature (71 stations) and precipitation measurements (232 stations) from the Federal Office of Meteorology and Climatology (Federal Office of Meteorology and Climatology, 2016), and a DEM with a resolution of 100 m derived from the DEM25 of the Federal Office of Topography (2015).

Future climate was predicted for a corresponding 24-year period from 2077 to 2100 (henceforth referred to as "2100") using modelled climate data from EURO-CORDEX, the European domain of the CORDEX project (http://euro-cordex.net). We selected three global climate models (GCMs): (1) CNRM-CERFACS-CNRM-CM5, (2) ICHEC-EC-EARTH and (3) MPI-M-MPI-ESM-LR, each downscaled with the regional climate model (RCM) CLMcom-CCLM4-8-17 by the CLMcom modelling group. These three model chains were selected to represent a broad range of possible climatic conditions for Switzerland at the end of the century. Whereas model chain (1) predicts a moderate increase in temperature, (2) is characterized by a marked temperature increase and drier summers than in (1) and (3). In model chain (3), precipitation in summer is lower but winter precipitation is higher than in the other two model chains (Appendix S1). For each of the three model chains, we considered two greenhouse gas concentration trajectories (Representative

TABLE 1 Topography, land cover and climate variables and their ecological significance for the mountain hare (*Lepus timidus*), as suggested in previous studies

Category	Variable	Description	Significance for mountain hare
Topography	Slope	Slope (°)	Indicator for habitat accessibility (Gilcrease, 2013)
	Topex	Topographic exposure index indicating a point's position relative to the surrounding terrain measured within a fixed distance of 150 m (Topex 150) for each of the eight cardinal directions	Indicator for the availability of resting sites from which hares can detect terrestrial predators early enough (unpublished data)
	Relief roughness	Topographic ruggedness index, which expresses the sum change in elevation between a grid cell and its eight neighbouring grid cells	Indicator for possibilities of escape from predator (Gilcrease, 2013)
	Distance to summit	Distance to sites where the sum of the angles to the ground within 1,000 m (Topex 1000), measured for each of the eight cardinal directions is ≥150 (m)	Indicator of wind and melt/freeze exposure (Yandow, Chalfoun, & Doak, 2015)
Land cover	Alpine grassland	Proportion of meadows, pastures, alpine grasslands, other grasses, shrubs and herbaceous vegetation (%)	Indicator for food availability (Bisi et al., 2013; Caravaggi et al., 2015; Rehnus et al., 2013; Wilkening et al., 2011)
	Bush cover	Proportion of bushes (%)	Indicator for food availability and hiding elements (Acevedo et al., 2012; Bisi et al., 2013; Rehnus et al., 2013)
	Forest cover	Proportion of forests (%)	Indicator for food availability and hiding elements (Acevedo et al., 2012; Caravaggi et al., 2015; Rehnus et al., 2013)
	Distance to forest edge	Distance to outer forest edges; calculated only for elevations above 1,300 m a.s.l., which corresponds to the lowest elevation at which mountain hares occur in the Alps (Rehnus, 2013) (m)	Distance to hiding elements (Caravaggi et al., 2015; Gilcrease, 2013; Rehnus et al., 2016)
	Glacier cover	Proportion of glaciers (%)	Absence of food and hiding elements (Rehnus, 2013)
	Moor cover	Proportion of moors (%)	Indicator for food availability and hiding elements (Hewson, 1990)
	Rock cover	Proportion of rocks (%)	Indicator for habitat accessibility and hiding elements (Bisi et al., 2013)
	Scree cover	Proportion of scree (%)	Indicator for hiding elements (Rehnus et al., 2013, 2016)
	Distance to creeks	Distance to creeks	Indicator for topographically suitable dispersal conditions (Gilcrease, 2013; Sokolov et al., 2009) or access to water resources in the case of low precipitation (Erb et al., 2011)
	Distance to roads	Distance to roads (m)	Indicator for human disturbance (Acevedo et al., 2012; Beever, Brussard, & Berger, 2003)
	Distance to anthropized areas	Distance to buildings with an area of at least 80 sqm (m)	Indicator for human disturbance (Acevedo et al., 2012; Gilcrease, 2013)
	Distance to ski lifts areas	Distance to ski lifts and cableways (m)	Indicator for human disturbance in winter (Rehnus et al., 2014)
Climate	Winter solar radiation	Sum of daily solar radiation (h) between December and February	Indicator for climatic favourability
	Summer solar radiation	Sum of daily solar radiation (h) between June and August	Indicator for heat stress (Acevedo et al., 2015; Beever, Ray, Mote, & Wilkening, 2010; Wilkening et al., 2011; Yandow et al., 2015; Yang, 1990)
	Temperature during the reproductive season	Average daily temperatures (°C) between April and August	Indicator for heat stress or exposure of juveniles to cold temperatures (Jansson & Pehrson, 2007; Rehnus, 2013)

(Continues)

TABLE 1 (Continued)

Category	Variable	Description	Significance for mountain hare
	Precipitation during the reproductive season	Sum of daily precipitation (mm) between April and August	Primary driver of pika persistence patterns in the Great Basin, for example, sustains plants communities pikas depend on (Erb et al., 2011); Indicator for mortality of juveniles in combination with cold temperatures during reproductive season (Rehnus, 2013)
	Length of vegetation growing season	Total # of days above 5°C, starting in spring after 6 days above 5°C and ending in autumn after 6 days below 5°C	Indicator for food growing conditions (Yandow et al., 2015)
	Reproductive season coldness	Total # of days with average temperature ≤5°C between April and August	More cold days are an indicator of increased chances of fertility due to decreased parasite loads (Newey & Thirgood, 2004; Newey et al., 2004)
	Summer warmth	Total # of days with average temperature ≥10°C between June and August	Indicator for heat stress (Acevedo et al., 2015; Beever et al., 2010; Wilkening et al., 2011; Yandow et al., 2015; Yang, 1990)
	Diurnal temperature range	Difference of monthly mean maximum and minimum temperature	Indicator for climatic temperature range (Acevedo et al., 2012, 2015)
	Seasonality of precipitation	Precipitation seasonality (coefficient of variation as a measure of climatic stability)	Indicator for climatic favourability (Acevedo et al., 2012, 2015)
	Winter precipitation	Sum of daily precipitation (mm) between December and February	Indicator for food availability and hiding elements in winter (Jansson & Pehrson, 2007)

Concentration Pathways, RCPs), RCP 4.5 and RCP 8.5, as adopted by the Fifth Assessment Report (AR5) of the IPCC (IPCC, 2014). This resulted in six possible paths of climate change, henceforth referred to as "climate change variants." Whereas RCP 4.5 represents a moderate pathway in which emissions peak around 2,040 and decline thereafter, the more extreme RCP 8.5 assumes that emissions continue to rise throughout the century (IPCC, 2014). The EURO-CORDEX data have a resolution of 0.11 degrees (EUR-11, ~12.5 km), which was much too coarse for our purposes. We therefore used the change factor method (Anandhi et al., 2011) to further downscale the data to a resolution of 100 m. We chose the sampling period (1990–2013) as the reference period and used the previously created Daymet raster data as the high-resolution dataset.

2.3.4 | Variable preparation

All variables were prepared as raster maps with a resolution of 100 × 100 m in the Swiss map projection (EPSG 21781). We assigned to each grid cell the variable means calculated in a circular moving window of 400 m radius to adjust the resolution to that of the species data and to take into consideration the environmental conditions in an area corresponding to the average home range of the species (Nodari, 2006). The raster maps were calculated with ARCGIS 10.3 (ESRI, 2016).

2.4 | Modelling approach

We used a maximum entropy modelling approach, implemented in the software MAXENT (Phillips, Anderson, & Schapire, 2006) because it

is robust with regard to collinearity problems (Dormann et al., 2013) and able to process presence-only data (Phillips et al., 2006). MAXENT is a machine-learning technique that contrasts the conditions at the species' locations with those prevailing throughout the study area by applying the principles of maximum entropy (for detailed information, see Elith et al., 2006; Phillips et al., 2006). Models were fitted using the default settings, that is, linear, quadratic, product, threshold and hinge features, a random background sample of 10,000 cells, a maximum of 500 iterations and a convergence threshold of 10^{-5}. Their accuracy was evaluated using the area under the receiver-operating characteristics curve AUC (Phillips et al., 2006). As no absence data were available, AUC statistics were calculated on the random background cells instead (Phillips et al., 2006). In this case, AUC values reflect the model's ability to discriminate between presence and random rather than between presence and absence, and the maximum achievable AUC is <1 (Phillips et al., 2006; Raes & Ter Steege, 2007).

In a first step, the topographic and land-cover variables (Table 1) were tested for collinearity. Of the pairs or groups of variables that were highly correlated (Spearman's $r \geq |.7|$; Dormann et al., 2013), we retained the one that best explained the presence of mountain hares in univariate models. Climate variables were tested for collinearity but not selected a priori (Appendix S2). Where the causal relationships with species presence are unknown, models including all potentially relevant climate variables have been shown to deliver more robust results (Braunisch et al., 2013).

We used a stepwise backward-forward selection approach to identify the most parsimonious model. For each step, we used 70% of the samples as training data and 30% as test data, applying the

random seed option to ensure that two iterations never used exactly the same training and test data. Starting with the full model, we sequentially removed the variable that contributed least to the model's predictive accuracy, as measured by the AUC calculated on the test data. The process was stopped once the AUC decreased following the removal of a variable. To the resulting "minimal model," we added each of the previously discarded variables in turn to ensure that none of them improved model performance.

The importance of each of the retained variables was assessed as the per cent contribution to the total increase in regularized log likelihood (gain) of the maximum entropy model compared to a uniform distribution provided by this variable (Phillips, 2016). In addition, we calculated the "permutation importance" for which the values of that variable on the presence and background data were randomly permuted, and the resulting drop in training AUC normalized to percentages was calculated (Phillips, 2016).

The final model was evaluated using 10-fold cross-validation and projected to the future climate conditions of 2100 for each of the six climate change variants, under the assumption that species-habitat associations remained temporally stable. We did not allow extrapolations to climatic conditions beyond the range found in the background data under current climate by treating variables with values outside the calibration range as if they were at the limit of the calibration range ("clamping," Elith, Kearney, & Phillips, 2010). This conservative approach avoids unrealistic predictions under future conditions, but may also lead to underestimating the "true" extent of the species' response (positive or negative) to future conditions. We therefore produced a map showing where clamping has been applied and predictions must be treated with caution (Appendix S3). In addition, we performed a multivariate environmental similarity surface (MESS) analysis (Elith et al., 2010) to show the multivariate similarity of each point of the study area under future climate conditions to the environmental range measured under current conditions (Appendix S4).

To discriminate between "suitable" and "unsuitable" habitat patches, we reclassified the MAXENT logistic output into binary "presence–absence" predictions using the threshold at which the sum of sensitivity and specificity calculated on the test data (averaged over the 10 cross-validation replicates) was maximized.

To subsequently evaluate overall connectivity and the importance of each habitat patch for connectivity in the Swiss Alps, we generated ensemble predictions by averaging the predictions of the three model chains under RCP 4.5 into ensemble 4.5, and the three model chains under RCP 8.5 into ensemble 8.5. The resulting ensemble maps were classified into binary "presence–absence" predictions using the same type of threshold (maximizing sensitivity plus specificity) averaged across the three models included.

2.5 | Distribution change

We compared the predicted area of mountain hare occurrence under current climate conditions with all six variants of potential future climate, both across the whole Swiss Alps and for each biogeographic region separately to elucidate regional patterns of distribution change. To explore the causes of these differences, we plotted the average regional conditions and predicted changes of the most important climatic predictors (selected according to their contribution to the final model) in relation to the species' response curve.

2.6 | Change in patch number, size and inter-patch distances

To analyse changes in number, patch size, inter-patch distance and connectivity, we considered only the suitable habitat patches larger than the average home range of a mountain hare (57.5 ha Nodari, 2006). To detect aggregations of suitable habitat patches, we smoothed the patches by applying a neighbourhood statistic retaining only cells for which a minimum of four out of their eight neighbours were classified as suitable.

We compared patch number and patch size (mean, median and 1st and 3rd quartiles) for the Swiss Alps and the biogeographic regions under all six climate change variants. Next-neighbour distances were classified into three categories (<1 km, 1–2 km and >2 km) according to the known average dispersal distance of mountain hares (1–2 km: Dahl & Willebrand, 2005; Harrison, 2011; Leach, Kelly, Cameron, Montgomery, & Reid, 2015; Nodari, 2006).

2.7 | Importance of habitat patches for connectivity

To assess the overall connectivity of the mountain hare habitat network in the Swiss Alps, we used the Integral Index of Connectivity (IIC) and the Equivalent Connected Area of the IIC (ECA (IIC)) calculated using the software CONEFOR SENSINODE 2.6 (Saura & Torne, 2009). Among the various connectivity metrics, the IIC is recommended because it integrates habitat amount and connectivity between habitat patches into a single metric (Pascual-Hortal & Saura, 2006). The IIC ranges from 0 to 1 (1 = an ideal landscape consisting only of habitat), and increases with improved connectivity. The ECA (IIC) makes it easy to interpret changes because it has the same unit as the attributes of the patches (here: square kilometre). The ECA (IIC) is defined as the size of a single habitat patch (maximally connected) that would provide the same IIC value as the actual habitat pattern in the landscape (Saura, Estreguilb, Moutonb, & Rodríguez-Freireb, 2011).

The relative contribution of each patch to overall habitat connectivity in the Swiss Alps was expressed by the delta of IIC (dIIC). The dIIC is defined as the relative decrease (in per cent) in the IIC value caused by the removal of the respective patch, taking into account (1) the area of the patch, (2) the estimated dispersal fluxes through that patch and (3) the importance of the patch as a connecting element (Pascual-Hortal & Saura, 2006). A sum of dIIC values (ΣdIIC) >100 across all patches indicates that one or more patches critical for connectivity can be found in the landscape (Saura & Pascual-Hortal, 2007). For example, if the loss of any key linking patch resulted in the remaining habitat being split into two disconnected networks, this node would cause a large decrease in habitat availability (Saura

& Pascual-Hortal, 2007). To identify isolated habitat patches, as well as key connector-patches, we used the connector fraction of the IIC (dIICconn), where a value of zero indicates isolation (Baranyi et al., 2011). Finally, to identify habitat patches with priority for habitat management today, we estimated the site overlap of currently suitable patches with those under future climate conditions.

Connectivity among patches was calculated in terms of Euclidean edge-to-edge distances using the extension "Conefor inputs" for ARCGIS 10.x (Saura & Torne, 2009). We excluded connections exceeding the maximum natal dispersal distance of 12 km of mountain hares (Hewson, 1990). We also excluded connections crossing slopes ≥70°, as they are considered as barriers for mountain hares. In addition, since we had only information about habitats within Switzerland, the dIICconn values of patches at the border of Switzerland were not considered.

3 | RESULTS

3.1 | Distribution change

Out of the 26 variables considered, 11 were retained in the final model (Table 2). With a mean test AUC of 0.787 ($SD = 0.018$), the model provided an acceptable discrimination between occupied and non-occupied mountain hare habitats according to the classification of Hosmer and Lemeshow (2000). The temperature during the reproductive season, relief roughness and the reproductive season

coldness were identified as the most important variables (Table 2). Together, they accounted for 64% of the total model gain and 68% of the permutation importance.

The predicted area of mountain hare habitat in the Swiss Alps decreased on average by 26% or an equivalent of 2,250 km^2 under RCP 4.5 and by 45% or an equivalent of 3,880 km^2 under RCP 8.5 by 2100 (Table 3). All six climate change variants consistently predicted a decline in habitat availability, with a minimum loss of 21% and a maximum loss of 55% in the Swiss Alps. The greatest average habitat loss among the three investigated biogeographic regions was predicted for the Northern Swiss Alps (RCP 4.5: −43%, RCP 8.5: −71%; maximum: −76%), followed by the Southern Swiss Alps (RCP 4.5: −21%, RCP 8.5: −41%; maximum: −50%) and the Central Swiss Alps (RCP 4.5: −19%, RCP 8.5: −33%; maximum: −47%).

The main reason for the predicted habitat loss is the expected increase in temperature during the reproductive season, which, under most climate change variants, was predicted to exceed by far the species' optimum of 7.5°C, particularly in the Northern and Southern Swiss Alps (Figure 2).

3.2 | Change in patch number, size and inter-patch distances

There was a great variance in patch number, size and inter-patch distances under both current and future conditions, with consistent trends in changes under the two RCPs: The predicted number of

TABLE 2 Variables retained in the best model for predicting the distribution of *Lepus timidus* across the Swiss Alps and their mean values at presence and background locations. Predictor importance is given as the percentage contribution to the total increase in regularized log likelihood compared to a uniform distribution averaged across the replicates of a 10-fold cross-validation. For "permutation importance," the variable values at training for presence and random locations were randomly permuted and the corresponding loss in training AUC (Area under the receiver operating characteristic curve, normalized as percentages) is given. Mean AUC and standard deviation (*SD*) across the cross-valdiation replicates are given. Variable definitions are presented in Table 1. Symbols indicate a positive (+), negative (−) or unimodal relationship (∩/U)

Variable	Per cent contribution	Permutation importance	Response type	Mean ± *SD* at locations	
				Presence	Random
Temperature during the reproductive season	36.2	11.0	∩	6.9 ± 2.6	8.6 ± 4.5
Relief roughness	18.9	22.1	∩	3.1 ± 0.5	3.1 ± 0.9
Reproductive season coldness	8.5	34.7	∩	55.9 ± 23.6	46.2 ± 34.3
Precipitation during the reproductive season	7.4	8.1	−	722.9 ± 198.9	781.2 ± 202.9
Distance to forest edge	7.0	3.5	−	582.1 ± 829.0	929.0 ± 1,297.5
Alpine grassland	6.9	1.7	+	0.5 ± 0.3	0.4 ± 0.3
Seasonality of precipitation	6.7	7.3	U	25.8 ± 9.0	24.8 ± 8.4
Summer warmth	3.7	3.1	∩	48.0 ± 21.1	57.5 ± 28.6
Distance to summit	3.1	4.4	−	457.4 ± 384.4	630.8 ± 694.2
Distance to creeks	1.0	2.3	−	293.1 ± 243.4	329.5 ± 371.8
Winter solar radiation	0.6	1.9	+	3909.8 ± 872.8	3674.3 ± 840.1
Mean training AUC ± *SD*	0.809 ± 0.002				
Mean test AUC ± *SD*	0.787 ± 0.018				
Number of variables	11				

TABLE 3 Predicted area of mountain hare habitat in the Swiss Alps under current and future (2100) climate conditions. Future habitat is predicted for the representative concentration pathways RCP 4.5 and RCP 8.5 (IPCC, 2014); each represented by three global climate model chains (1) CNRM-CERFACS-CNRM-CM5-CLMcom-CCLM4-8-17, (2) ICHEC-EC-EARTH-CLMcom-CCLM4-8-17 and (3) MPI-M-MPI-ESM-LR-CLMcom-CCLM4-8-17. Maximum changes between current and future distributions per region are marked in bold

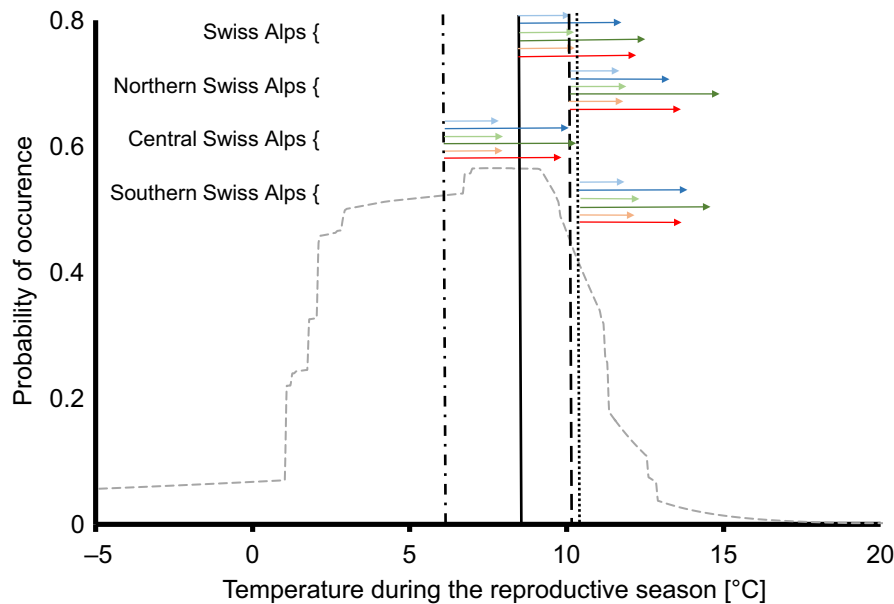| Climate data	RCP	Swiss Alps Suitable area (km²)	Unsuitable area (km²)	(%)	Northern Swiss Alps Suitable area (km²)	Unsuitable area (km²)	(%)	Central Swiss Alps Suitable area (km²)	Unsuitable area (km²)	(%)	Southern Swiss Alps Suitable area (km²)	Unsuitable area (km²)	(%)	Habitat loss by 2100 compared to the current situation (%) Swiss Alps	Northern Alps	Central Alps	Southern Alps
Weather station data (1990–2013) interpolated using DAYMET	–	8,715	17,087	33.8	2,497	8,981	27.8	5,479	5,175	51.4	738	2,923	25.2	–	–	–	–
CNRM-CERFACS-CNRM-CM5-CLMcom-CCLM4-8-17 (2077–2100)	4.5	5,765	20,038	22.3	1,293	10,185	12.7	3,881	6,773	36.4	590	3,071	19.2	–33.9	–48.2	–29.2	–20.0
	8.5	3,883	21,920	15.0	590	10,888	5.4	2,911	7,743	27.3	381	3,281	11.6	**–55.4**	**–76.4**	**–46.9**	–48.4
ICHEC-EC-EARTH–CLMcom-CCLM4-8-17 (2077–2100)	4.5	6,847	18,956	26.5	1,530	9,948	15.4	4,739	5,915	44.5	578	3,084	18.7	–21.4	–38.7	–13.5	–21.7
	8.5	4,866	20,936	18.9	676	10,801	6.3	3,822	6,832	35.9	367	3,294	11.1	–44.2	–72.9	–30.3	**–50.3**
MPI-M-MPI-ESM-LR–CLMcom-CCLM4-8-17 (2077–2100)	4.5	6,783	19,019	26.3	1,422	10,056	14.1	4,776	5,878	44.8	585	3,077	19.0	–22.2	–43.0	–12.8	–20.8
	8.5	5,757	20,045	22.3	909	10,569	8.6	4,288	6,366	40.2	559	3,103	18.0	–33.9	–63.6	–21.7	–24.3
Average habitat loss by 2100 as compared to the current situation under IPCC scenario 4.5														–25.8	–43.3	–18.5	–20.8
IPCC scenario 8.5														–44.5	–71.0	–33.0	–41.0

FIGURE 2 Relative probability of mountain hare occurrence (as MAXENT logistic output; dashed grey line) as a function of the average temperature during the reproductive season. The vertical lines show the average conditions in mountain hare habitats under current climate conditions (black line = Swiss Alps, dotted line = Northern Swiss Alps, point-dot line = Central Swiss Alps, dashed line = Southern Swiss Alps). Arrows indicate the predicted changes by 2100 under the six climate change variants as defined in the section "climate." Light colours illustrate model chains under RCP 4.5, and dark colours the corresponding chains under RCP 8.5 (light/dark blue = CNRM-CERFACS-CNRM-CM5–CLMcom-CCLM4-8-17 & RCP 4.5/8.5; light/dark green = ICHEC-EC-EARTH–CLMcom-CCLM4-8-17 & RCP 4.5/8.5; light/dark red = MPI-M-MPI-ESM-LR–CLMcom-CCLM4-8-17 & RCP 4.5/8.5)

habitat patches in the Swiss Alps increased on average by 25% (118 patches, SD = 54) under climate change variants with RCP 4.5, and by 80% (38 patches, SD = 91) under climate change variants with RCP 8.5 (Appendix S5). In contrast, patch size decreased by an average of 40% (765 ha, SD = 184 ha) and of 46% (888 ha, SD = 293 ha) under variants 4.5 and 8.5, respectively. Changes in patch number, size and inter-patch distance varied significantly among the Northern, Central and Southern Swiss Alps, with changes being more pronounced at the edges of the mountain hare distribution range (Table 4; Appendices S5 and S6). Currently, habitat patches vary considerably in size and nearest-neighbour distance, and differ across regions. The average patch size in the Swiss Alps is 1,929 ha (SD = 16,026), ranging from 656 to 4,693 ha across regions (Table 4; details Appendix S5). The respective values for nearest-neighbour distances are 538 m (SD = 551), ranging from 387 to 735 m (Table 4; details Appendix S6).

3.3 | Importance of habitat patches for connectivity

The overall connectivity index values (IIC) in the Swiss Alps decreased from 0.041 to 0.013 under ensemble 4.5 and to 0.009 under ensemble 8.5. The ECA (IIC) decreased by 45% from 5,253 to 2,911 km^2 under ensemble 4.5, and by 53% to 2,479 km^2 under ensemble 8.5.

The number of habitat patches critical for connectivity also increased, with increasing ΣdIIC from 173% to 182% under ensemble 4.5, and to 196% under ensemble 8.5. Patch-dIIC was strongly

correlated with patch size (Pearson's r = .99) under current conditions and the two future projections. The maximum estimated dIIC of a patch was 72% in the current situation, 85% under ensemble 4.5 and 40% under ensemble 8.5. The most important patches were consistently located in the eastern part of the Central Swiss Alps (Figure 3a–c).

The proportion of suitable but isolated patches (dIICconn = 0) and their percentage area increased from 49% and 17% (patch area 888 km^2; average patch size: 4 km^2) in the current situation to 66% and 51% under ensemble 4.5 (patch area 1,474 km^2; average patch size: 4 km^2) and to 51% and 32% under ensemble 8.5 (patch area 804 km^2; average patch size: 3 km^2; Figure 3).

We found that future sites of suitable patches overlapped considerably with those observed in the present. Thus, 92% of the habitat predicted under climate change variant RCP 4.5 overlapped with current habitat, and 82% under RCP 8.5. This, in combination with the spatial distribution of future mountain hare occurrence (Figure 3), suggests that habitat is more likely to contract at the higher elevations, than to expand to areas beyond the current range (Figure 3).

4 | DISCUSSION

Our models predict a loss of habitat area and an increase in habitat fragmentation for the mountain hare under climate change. In particular, they predict a reduction in the amount of suitable habitat, an

TABLE 4 Average changes in number, size and inter-patch distance of mountain hare habitat patches in the Swiss Alps under future predicted (2100) climate conditions assuming the representative concentration pathways RCP 4.5 and RCP 8.5 (IPCC, 2014), compared to the current situation. The details of changes are given in Appendices S5 and S6

Variable	Climate condition	RCP	Swiss Alps Mean ± SD	Northern Swiss Alps Mean ± SD	Central Swiss Alps Mean ± SD	Southern Swiss Alps Mean ± SD
Patch number (N total)	Current situation	–	465	245	120	114
	Changes by 2100	4.5	118 ± 54	51 ± 7	92 ± 32	−28 ± 16
		8.5	38 ± 91	−52 ± 13	128 ± 71	−35 ± 21
Patch size (ha)	Current situation	–	1,929 ± 16,026	1,052 ± 2,810	4,693 ± 28,774	656 ± 2,002
	Changes by 2100	4.5	−765 ± 184	−565 ± 48	−2,433 ± 490	54 ± 108
		8.5	−888 ± 293	−690 ± 65	−2,973 ± 631	−62 ± 152
Inter-patch distance (m)	Current situation	–	538 ± 551	515 ± 498	387 ± 303	735 ± 743
	Changes by 2100	4.5	161 ± 33	293 ± 55	91 ± 6	197 ± 68
		8.5	201 ± 51	719 ± 73	102 ± 57	3 ± 274

increase in the number of habitat patches, a decrease in the size of habitat patches, an increase in inter-patch distance and a decrease in overall habitat connectivity. These changes were generally more pronounced for the greenhouse gas concentration trajectory RCP 8.5 than for RCP 4.5.

4.1 | Distribution change

The current distribution of mountain hare is mainly determined by the average ambient temperature during the reproductive season, with an optimum between 7 and 9°C. The climate change-induced increase in temperature beyond this optimum is the main driver for the predicted loss of suitable habitat by the year 2100. According to predictive distribution models worldwide, increasing temperatures will force Alpine and Arctic species to seek cooler temperatures at higher elevations or at the poleward edges of continents (e.g. Beever et al., 2011; Büntgen et al., 2017; Moritz et al., 2008; Pedersen, Odden, & Pedersen, 2017; Pernollet et al., 2015). This is because Alpine and Arctic species living at the warmer margins of their bioclimatic niches are especially vulnerable to physiological stress, such as an inability to thermoregulate during especially warm periods (e.g. Moritz et al., 2008; Parmesan, 2006; Wilkening et al., 2011). In the Swiss Alps, the potential for animals to compensate for range losses at lower elevations by expanding upwards is limited by the shape and height of the mountains. As a result, the potential habitat area decreases with increasing elevation (Pepin et al., 2015).

We found that the decline in the number of days with an average temperature ≤5°C during the reproductive period had a negative influence on the probability of occurrence of the mountain hare. This pattern might be explained by a higher parasite load, as parasites such as nematodes and coccidia are more likely to thrive under warmer conditions, and thus negatively impact the health and/or fecundity of mountain hares (Newey & Thirgood, 2004; Newey, Thirgood, & Hudson, 2004). Although these studies refer to Scottish moorland where excessive grouse habitat management and associated predator control can lead to very high hare densities and in turn parasite

loads, similar effects have been found for other species of Alpine and Arctic environments, including caribou *Rangifer tarandus* (Albon et al., 2002; Descamps et al., 2017), musk oxen *Ovibos moschatus* (Kutz, Hoberg, Polley, & Jenkins, 2005), Rock Ptarmigan (Stenkewitz, Nielsen, Skirnisson, & Stefansson, 2016) and Soay sheep *Ovis aries* (Gulland, Albon, Pemberton, Moorcroft, & Cluttonbrock, 1993). Alternatively, hares might prefer cold days during the reproductive season as persisting snow could reduce predation risk due to a better colour match of the fur with the environment (see Mills et al., 2013; Pedersen et al., 2017; Zimova, Mills, & Nowak, 2016). In the Alps, however, the coat colour change from white to brown is mostly finished by the end of May when the first litter of the same year occurs (Slotta-Bachmayr, 1998; Thulin & Flux, 2003). It remains unclear, whether this may already reflect a climate-change-induced mismatch, given the hare's limited phenotypic plasticity to adapt its seasonal camouflage (e.g. Zimova et al., 2016). Thus, further research is needed to clarify why mountain hares need cold temperatures during the breeding period.

Finally, European hares (*Lepus europaeus*), which occupy a similar niche in the lower altitudes of the study region (Hackländer & Jenny, 2011), may benefit from increasing temperatures and expand their range to higher elevations (Hackländer & Jenny, 2011), which may lead to interspecific competition (Caravaggi, Montgomery, & Reid, 2015; Caravaggi et al., 2017; Jansson & Pehrson, 2007; Reid, 2011; Thulin, 2003) or even introgression (Zachos et al., 2010) with mountain hares. Since our model does not include interspecific interactions, we cannot exclude the possibility that the observed pattern may be influenced by competitive exclusion.

Our predictions for habitat loss of the mountain hare in the Swiss Alps by 2100 are in line with predictions of the decline of other mountain hare populations throughout Europe (Eurasia: Leach et al., 2015; Europe: Acevedo, Jiménez-Valverde, Melo-Ferreira, Real, & Alves, 2012; Italy: Bisi, Wauters, Preatoni, & Martinoli, 2015; UK: Anderson et al., 2009; Ireland: Caravaggi et al., 2015; Sweden: Elmhagen, Kindberg, Hellström, & Angerbjörn, 2015; Jansson & Pehrson, 2007; Thulin, 2003; Norway: Pedersen et al., 2017). However, the magnitude of loss
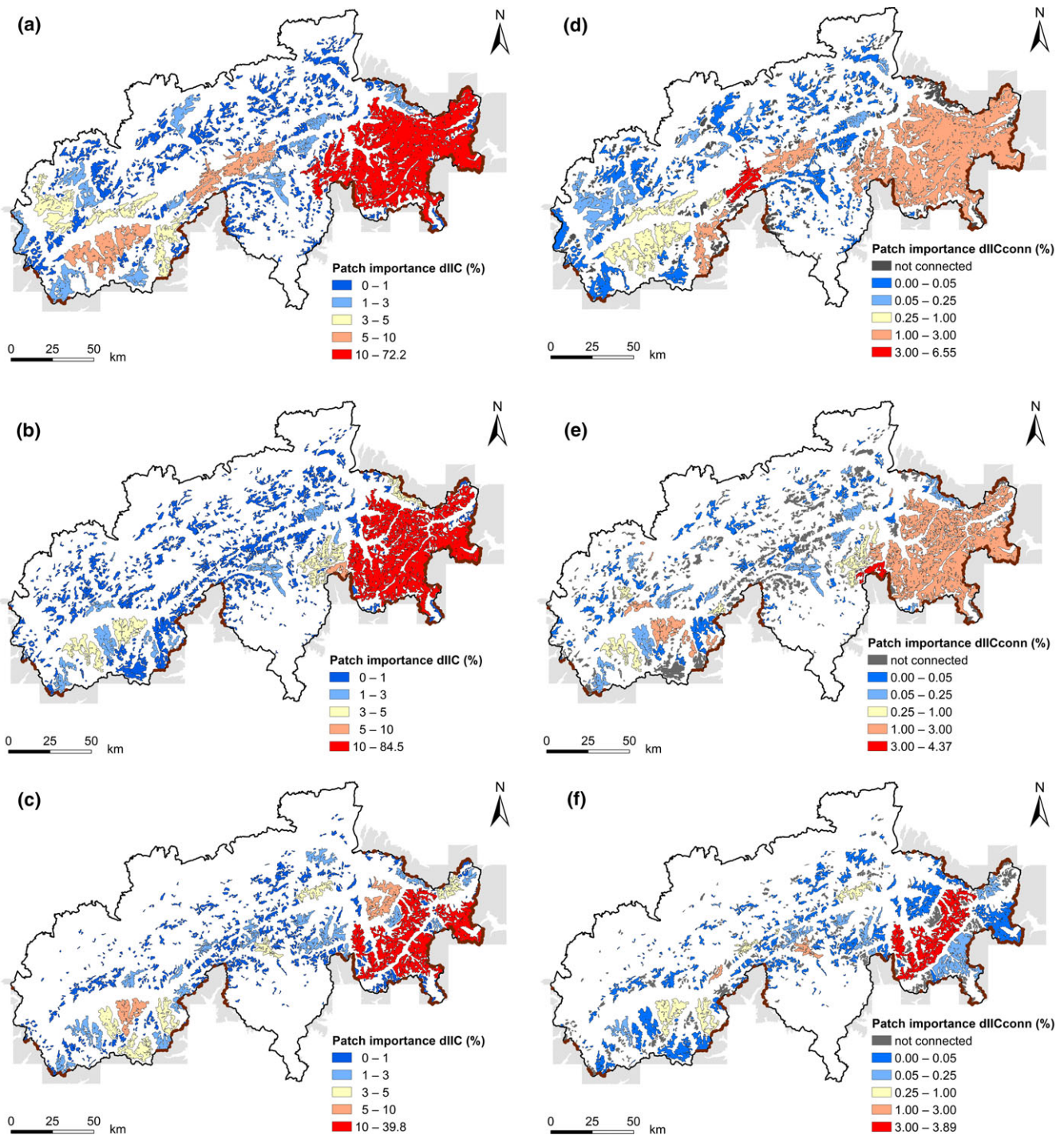
FIGURE 3 Predicted mountain hare habitat and the relative importance of the patches for overall habitat connectivity (measured by the Integral Index of Connectivity IIC) under current conditions (a, d; IIC = 0.041), under ensemble 4.5 (b, e; IIC = 0.013) and under ensemble 8.5 (c, f; IIC = 0.009) in the Swiss Alps (black line). Patch importance is given as the per cent decrease in total IIC (dIIC, left) when removing the respective patch, and the decrease in the connector fraction of the IIC (dIICconn, right). The importance of patches along the borders of Switzerland (brown; current situation: $N = 24$, ensemble 4.5: $N = 36$, ensemble 8.5: $N = 56$) is not considered as they might be connected with habitat patches outside the study area (light grey, elevation ≥1,300 m a.s.l.)

predicted for the Swiss Alps by 2100 between −26% (RCP4.5) and −45% (RCP8.5) is much higher than that predicted by 2070 for the Sondrio region in the Italian Alps (−3%; Bisi et al., 2015), a region bordering on the southeastern part of the Swiss Alps. This discrepancy is not only due to the climate data sources and the higher spatial accuracy of the species data in our study, but also mainly to the integration of species-relevant, high-resolution land-cover information. Including this information led to a more realistic restriction of the future "climatic envelope" to those areas actually offering suitable landscape conditions.

The predicted changes vary among the three biogeographic regions, and habitat loss is expected to be much higher in the Northern and Southern Alps than in the Central Alps. The two latter regions are situated at the edge of the species' distribution, which may explain this pattern (e.g. Anderson et al., 2009; Beever, Dobrowski, Long, Mynsberge, & Piekielek, 2013; Calkins et al., 2012). However, the relative habitat loss is twice as high in the Northern as in the Southern Alps. The reason for this difference could be that the patches in the Southern Swiss Alps are closer to the habitats of highest importance for overall habitat connectivity, that is, better connected to the main population than those in the Northern Alps (Figure 3a,d).

4.2 | Change in patch number, size and inter-patch distances

Under climate change, the average number of habitat patches in the Swiss Alps is predicted to increase. At the same time, patches are likely to decrease in size and increase in inter-patch distance, which corresponds to the definition of increased habitat fragmentation (Fahrig, 2003). The increased inter-patch distances in all three biogeographic regions may specially reduce the likelihood of successful movement, reproduction and therefore gene flow among subpopulations (Reed & Frankham, 2003; Rudnick et al., 2012; Van Strien et al., 2014).

The changes in the size and number of patches vary greatly in the three regions. In the Central Swiss Alps, we predict a decrease in patch size paralleled by an increase in patch numbers which suggests that existing large patches become more fragmented. In the Northern Swiss Alps, we expect the number of patches to remain similar to the current number, but with smaller sizes with greater inter-patch distances as the result of the shrinkage of existing patches. In the Southern Swiss Alps, fewer patches are likely, but with sizes similar to those in the current situation. This suggests that the increased inter-patch distances are mainly due to the loss of small patches connecting the low number of existing large patches. Relatively high amounts of precipitation are predicted during the breeding period in the North and the South, which may also lead to higher mortality among young hares (Kielland, Olson, & Euskirchen, 2010). We therefore expect that the mountain hare populations in the Northern and Southern Swiss Alps, which have lower densities than those in the population in the Central Alps (Rehnus et al., 2016), will suffer more quickly from the negative effects associated with fragmentation (e.g. inbreeding, vulnerability to stochastic events) and thus face a higher risk of extinction, unless they are connected to neighbouring populations in France, Austria or Italy.

4.3 | Importance of habitat patches for connectivity

According to our graph-theory models, the overall habitat connectivity for mountain hares will substantially decrease in the Swiss Alps by 2100 under both IPCC scenarios RCP 4.5 and RCP 8.5. This is reflected in a decrease in ECA (IIC) by nearly half of the current habitat area, and an increase in both the proportion of isolated patches and habitats critical for connectivity. The sum of dIIC values under the current situation is already >100 across all patches, indicating that patches critical for connectivity already exist in the landscape. The spatial alignment of important patches for connectivity from East to West indicates the importance of the habitat corridor along the central Alpine mountain range, which is not only crucial for maintaining habitat connectivity today, but will also be essential under both future climate scenarios. This Swiss mountain range may also have a vital connectivity function for mountain hare populations throughout the entire Alpine arch, from France to Austria, as we identified some important patches at the eastern, western and southern borders of the study area (e.g. in Goms, Hinterrhein, Rätikon and Engadine). These important habitat patches are connected to other suitable areas in the neighbouring mountain regions outside the study area. Connectivity analyses across the entire Alpine Arc may further elucidate this aspect and may reduce uncertainties in current predictions of future mountain hare distributions in the Alps under climate change.

Larger patches will be, as we predict, more important than smaller ones in their overall contribution to connectivity (dIIC) and to the connecting function (dIICconn) alone, in particular if we continue to consider patch size to be a reasonable surrogate for the landscape's carrying capacity for the species (Van Der Wal, Shoo, Johnson, & Williams, 2009). Studies of gene flow and demographic parameters are needed to understand how connectivity and source–sink dynamics influence dynamic species range models, as well as the population viability of the mountain hare population in particular (Schurr et al., 2012).

We found a considerable overlap between current and predicted habitat patches, indicating areas, where we can expect an above average probability of population persistence. Species conservation measures, such as hunting limitations and habitat improvement, may partly compensate the negative effects of climate change in the future (see below and also Bollmann & Braunisch, 2016; Braunisch et al., 2014). They are likely to be most effective in these overlap areas because they cover the bioclimatic requirements of the mountain hare under current and predicted conditions.

4.3.1 | Conservation aspects for Alpine and Arctic species

We showed that mountain hare populations in the Swiss Alps are threatened by habitat loss and fragmentation, with increasingly limited options for successful dispersal under climate change. We therefore recommend targeted conservation measures aiming at improving habitat quality and connectivity (Bollmann & Braunisch, 2016; Braunisch et al., 2014; Heller & Zavaleta, 2009; Rudnick et al., 2012). In this way, our results indicate that terrain roughness in combination with forest accessibility and grassland abundance positively affects mountain hare occurrence (Table 2), as this landscape configuration provides a diverse mosaic of food and protection in close distance (Rehnus et al., 2016). The ongoing

encroachment of forest on agricultural land in the Alps has been exacerbated by climate warming (Ceschi, 2006; Speich et al., 2011). Forest encroachment results in vegetation homogenization and the loss of structural diversity and habitat heterogeneity. It may therefore have negative consequences for mountain hares, similar to that found for other species in the Alpine treeline ecosystem (Bollmann, 2010; Braunisch, Patthey, & Arlettaz, 2016). Furthermore, for mountain hares and other Alpine and Arctic species, habitat quality has been shown to increase with structural heterogeneity (Patthey, Signorell, Rotelli, & Arlettaz, 2012; Schweiger et al., 2012; Signorell et al., 2010; Sokolov, Ivanitskaya, Gruzdev, & Heptner, 2009), mosaic-like configuration of forest habitats intermixed with dwarf shrubs, alpine pastures and basal-branched trees (Bollmann, Weibel, & Graf, 2005; Geary et al., 2013; Rehnus et al., 2016), high densities of large shrubs, saplings and medium-sized trees in the surrounding forest stands (Lewis, Hodges, Koehler, & Mills, 2011), and a mixture of both deciduous and coniferous trees in woodlands (Aberg, Swenson, & Angelstam, 2003; Hiltunen & Kauhala, 2006). Management approaches that forgo salvaging the effects of natural process dynamics (e.g. avalanches and storms) and forestry measures creating or facilitating the occurrence of the above-mentioned structures in multifunctional landscapes are therefore most likely to benefit the mountain hare as well as a considerable fraction of the community of Alpine species sharing requirements of semi-open mosaic habitats.

Activities for improving habitat quality should focus on patches with high importance for connectivity like within the identified corridor in the Central Swiss Alps, which connects eastern and western mountain hare populations. We assume that conservation activities in these patches would also enhance the population connectivity of other members of the Alpine community such as grouse species with similar habitat requirements at the upper timberline, which also occur as isolated glacial relict populations in the Alps and which are vulnerable to climate change (e.g. Bollmann & Braunisch, 2016; Braunisch et al., 2013, 2014; Furrer et al., 2016; Imperio, Bionda, Viterbi, & Provenzale, 2013; Pernollet et al., 2015).

Along with habitat improvement, we recommend reducing the expansion of winter recreational activities, particularly in patches crucial for maintaining population connectivity, and applying schemes for sustainable hunting. Winter recreational activities can cause Alpine species to abandon otherwise suitable habitats (e.g. Black grouse: Braunisch, Patthey, & Arlettaz, 2011; red deer *Cervus elaphus*: Coppes, Burghardt, Hagen, Suchant, & Braunisch, 2017), impacting physiology and behaviour and creating an extra demand for energy when food resources are scarce (e.g. Arlettaz et al., 2015; Rehnus et al., 2014).

Because climate change predictions are subject to high level of uncertainty (Elith & Leathwick, 2009), monitoring should be integrated into an adaptive management plan for sustainably harvesting and conserving the species. A recently developed non-invasive method based on sampling faeces should help to collect more data about mountain hare population dynamics and trends in the Alps (Rehnus & Bollmann, 2016) and also to monitor hybridization rates

(Beugin et al., 2017). Identifying changes in the abundance and distribution of peripheral populations of vulnerable Arctic and Alpine species can serve as an early threat indicator for ecologists and wildlife managers (Beever et al., 2013).

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REFERENCES

Aberg, J., Swenson, J. E., & Angelstam, P. (2003). The habitat requirements of hazel grouse (*Bonasia bonasia*) in managed boreal forest and applicability of forest stand descriptions as a tool to identify suitable patches. *Forest Ecology and Management*, *175*, 437–444.

Acevedo, P., Jiménez-Valverde, A., Melo-Ferreira, J., Real, R., & Alves, P. C. (2012). Parapatric species and the implications for climate change studies: A case study on hares in Europe. *Global Change Biology*, *18*, 1509–1519.

Acevedo, P., Melo-Ferreira, J., Farelo, L., Beltran-Beck, B., Real, R., Campos, R., & Alves, P. C. (2015). Range dynamics driven by Quaternary climate oscillations explain the distribution of introgressed mtDNA of *Lepus timidus* origin in hares from the Iberian Peninsula. *Journal of Biogeography*, *42*, 1727–1735.

Adrian, M. (2015). *Jagdzeiten wild*. Retrieved 12th August 2015, from www.schonzeit.de

Albon, S. D., Stien, A., Irvine, R. J., Langvatn, R., Ropstad, E., & Halvorsen, O. (2002). The role of parasites in the dynamics of a reindeer population. *Proceedings of the Royal Society B-Biological Sciences*, *269*, 1625–1632.

Anandhi, A., Frei, A., Pierson, D. C., Schneiderman, E. M., Zion, M. S., Lounsbury, D., & Matonse, A. H. (2011). Examination of change factor methodologies for climate change impact assessment. *Water Resources Research*, *47*, W03501.

Anderson, B. J., Akcakaya, H. R., Araujo, M. B., Fordham, D. A., Martinez-Meyer, E., Thuiller, W., & Brook, B. W. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B-Biological Sciences*, *276*, 1415–1420.

Arlettaz, R., Nussle, S., Baltic, M., Vogel, P., Palme, R., Jenni-Eiermann, S., . . . Genoud, M. (2015). Disturbance of wildlife by outdoor winter recreation: Allostatic stress response and altered activity-energy budgets. *Ecological Applications*, *25*, 1197–1212.

Baranyi, G., Saura, S., Podani, J., & Jordan, F. (2011). Contribution of habitat patches to network connectivity: Redundancy and uniqueness of topological indices. *Ecological Indicators*, *11*, 1301–1310.

Beever, E. A., Brussard, P. E., & Berger, J. (2003). Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *Journal of Mammalogy*, *84*, 37–54.

Beever, E. A., Dobrowski, S. Z., Long, J., Mynsberge, A. R., & Piekielek, N. B. (2013). Understanding relationships among abundance, extirpation, and climate at ecoregional scales. *Ecology*, 94, 1563–1571.

Beever, E. A., Ray, C., Mote, P. W., & Wilkening, J. L. (2010). Testing alternative models of climate-mediated extirpations. *Ecological Applications*, 20, 164–178.

Beever, E. A., Ray, C., Wilkening, J. L., Brussard, P. F., & Mote, P. W. (2011). Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology*, 17, 2054–2070.

Beugin, M.-P., Letty, J., Kaerle, C., Guitton, J.-S., Muselet, L., Queney, G., & Pontier, D. (2017). A single multiplex of twelve microsatellite markers for the simultaneous study of the brown hare (*Lepus europaeus*) and the mountain hare (*Lepus timidus*). *Ecology and Evolution*, 7, 3931–3939.

Bisi, F., Nodari, M., Dos Santos Oliviera, N. M., Masseroni, E., Preatoni, D. G., Wauters, L. A., … Martinoli, A. (2011). Space use patterns of mountain hare (*Lepus timidus*) on the Alps. *European Journal of Wildlife Research*, 57, 305–312.

Bisi, F., Nodari, M., Dos Santos Oliviera, N. M., Masseroni, E., Preatoni, D. G., Wauters, L. A., & Martinoli, A. (2013). Habitat selection and activity patterns in Alpine mountain hare (*Lepus timidus varronis*). *Mammalian Biology*, 78, 28–33.

Bisi, F., Wauters, L. A., Preatoni, D. G., & Martinoli, A. (2015). Interspecific competition mediated by climate change: Which interaction between brown and mountain hare in the Alps? *Mammalian Biology*, 80, 424–430.

Bollmann, K. (2010). Climate or land use change: What affects Alpine grouse species more? In E. Maselli (Ed.), *Biodiversity in time of climate change: Management or wilderness?* (pp. 28–32). Chambéry, France: ALPARC.

Bollmann, K., & Braunisch, V. (2016). Auswirkungen des Klimawandels auf Bergwaldvogelarten. In A. R. Pluess, S. Augustin & P. Brang (Eds) *Wald im Klimawandel. Grundlagen für Adaptationsstrategien* (pp. 287–309). Bundesamt für Umwelt BAFU, Bern, Switzerland; Eidg. Forschungsanstalt WSL, Birmensdorf, Switzerland: Haupt Verlag Bern.

Bollmann, K., Weibel, P., & Graf, R. F. (2005). An analysis of central Alpine capercaillie spring habitat at the forest stand scale. *Forest Ecology and Management*, 215, 307–318.

Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Schmid, H., & Bollmann, K. (2013). Selecting from correlated climate variables: A major source of uncertainty for predicting species distributions under climate change. *Ecography*, 36, 971–983.

Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Zellweger, F., & Bollmann, K. (2014). Temperate mountain forest biodiversity under climate change: Compensating negative effects by increasing structural complexity. *PLoS One*, 9, e97718.

Braunisch, V., Patthey, P., & Arlettaz, R. L. (2011). Spatially explicit modeling of conflict zones between wildlife and snow sports: Prioritizing areas for winter refuges. *Ecological Applications*, 21, 955–967.

Braunisch, V., Patthey, P., & Arlettaz, R. (2016). Where to combat shrub encroachment in Alpine timberline ecosystems: Combining remotely-sensed vegetation information with species habitat modelling. *PLoS One*, 11, e0164318.

Bundesamt Für Statistik (1997). *Arealstatistik der Schweiz 1992/97*. Retrieved 12th January 2016, from www.bfs.admin.ch/bfs/de/home/statistiken/raum-umwelt/erhebungen/area.html

Büntgen, U., Greuter, L., Bollmann, K., Jenny, H., Liebhold, A., Galván, J. D., … Mysterud, A. (2017). Elevational range shifts in four mountain ungulate species from the Swiss Alps. *Ecosphere*, 8, e01761.

Calkins, M. T., Beever, E. A., Boykin, K. G., Frey, J. K., & Andersen, M. C. (2012). Not-so-splendid isolation: Modeling climate-mediated range collapse of a montane mammal *Ochotona princeps* across numerous ecoregions. *Ecography*, 35, 780–791.

Caravaggi, A., Leach, K., Santilli, F., Rintala, J., Helle, P., Tiainen, J., … Reid, N. (2017). Niche overlap of mountain hare subspecies and the vulnerability of their ranges to invasion by the European hare; the (bad) luck of the Irish. *Biological Invasions*, 19, 655–674.

Caravaggi, A., Montgomery, W. I., & Reid, N. (2015). Range expansion and comparative habitat use of insular, congeneric lagomorphs: Invasive European hares *Lepus europaeus* and endemic Irish hares *Lepus timidus hibernicus*. *Biological Invasions*, 17, 687–698.

Centre Suisse De Cartographie De La Faune Cscf (2015). *Mountain hare – Lepus timidus*. Retrieved 13th October 2015, from www.cscf.ch

Ceschi, I. (2006). *Il Bosco del cantone Ticino*, Locarno, Bellinzona, Dipartimento del territorio, Divisione dell'ambiente, Sezione forestale, A. Dadò.

Coppes, J., Burghardt, F., Hagen, R., Suchant, R., & Braunisch, V. (2017). Human recreation affects spatio-temporal habitat use patterns in red deer (*Cervus elaphus*). *PLoS One*, 12, e017513.

Dahl, F., & Willebrand, T. (2005). Natal dispersal, adult home ranges and site fidelity of mountain hares *Lepus timidus* in the boreal forest of Sweden. *Wildlife Biology*, 11, 309–317.

Descamps, S., Aars, J., Fuglei, E., Kovacs, K. M., C., Lydersen, Pavlova, O., … Strøm, H. (2017). Climate change impacts on wildlife in a high Arctic archipelago – Svalbard, Norway. *Global Change Biology*, 23, 490–502.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46.

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129–151.

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1, 330–342.

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics*, 40, 677–697.

Elmhagen, B., Kindberg, J., Hellström, P., & Angerbjörn, A. (2015). A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. *Ambio*, 44, 39–50.

Elsen, P. R., & Tingley, M. W. (2015). Global mountain topography and the fate of montane species under climate change. *Nature Climate Change*, 5, 772.

Environment Agency Austria (2015). *Österreichisches Artenschutz-Informationssystem (Version 2.0)*. Retrieved 12th August 2015, from www.umweltbundesamt.at/umweltschutz/naturschutz/artenschutz/oasis

Erb, L. P., Ray, C., & Guralnick, R. (2011). On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology*, 92, 1730–1735.

Esri (2016). *ArcGIS 10.3*. Redlands, CA: ESRI.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, 34, 487–515.

Federal Office of Meteorology and Climatology (2016). *Climate diagrams and normal values per station*. Retrieved 23rd November 2016, from www.meteoschweiz.admin.ch

Federal Office of Topography (2015). *Vector 25*. Retrieved 1st October 2015, from www.swisstopo.admin.ch

Federal Statistical Office (1997). *Arealstatistik der Schweiz 1992/97*. Retrieved 13th October 2015, from www.bfs.admin.ch/bfs/de/home/statistiken/raum-umwelt/erhebungen/area/geschichte/area-1992-97.html

Fischer, J., & Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: A synthesis. *Global Ecology and Biogeography*, 16, 265–280.

Fourcade, Y., Engler, J. O., Rödder, D., & Secondi, J. (2014). Mapping species distributions with MAXENT using a geographically biased sample of presence data: A performance assessment of methods for correcting sampling bias. *PLoS One*, 9, e97122.

Furrer, R., Schaub, M., Bossert, A., Isler, R., Jenny, H., Jonas, T., ... Jenni, L. (2016). Variable decline of Alpine Rock Ptarmigan (*Lagopus muta helvetica*) in Switzerland between regions and sites. *Journal of Ornithology*, *157*, 787–796.

Galpern, P., Manseau, M., & Fall, A. (2011). Patch-based graphs of landscape connectivity: A guide to construction, analysis and application for conservation. *Biological Conservation*, *144*, 44–55.

Gamboni, A.-S. (1997). *Comportement spatio-temporel d`une population de lievre variable (*Lepus timidus varronis*) au sud des alpes*. Master thesis, University of Neuchâtel, Neuchâtel, 70 pp.

Geary, M., Fielding, A. H., & Marsden, S. J. (2013). Designing mosaic landscapes for Black Grouse *Tetrao tetrix* using multi-scaled models. *Ibis*, *155*, 792–803.

Gilcrease, K. (2013). An assessment of leporid research and landscape ecology metrics in a European landscape. *Journal of Landscape Ecology*, *6*, 1–17.

Gonseth, Y., Wohlgemuth, T., Sansonnens, B., & Buttler, A. (2001). *Die biogeographischen Regionen der Schweiz. Erläuterungen und Einteilungsstandard*. Bern, Switzerland: Federal Office for the Environment.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, *8*, 993–1009.

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., ... Buckley, Y. M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, *16*, 1424–1435.

Gulland, F. M. D., Albon, S. D., Pemberton, J. M., Moorcroft, P. R., & Cluttonbrock, T. H. (1993). Parasite-associated polymorphism in a cyclic ungulate population. *Proceedings of the Royal Society B-Biological Sciences*, *254*, 7–13.

Gutleb, B., Komposch, B., & Spitzenberger, F. (1999). Rote Liste der Säugetiere Kärntens (Vertebrata, Mammalia). In T. Rottenburg, C. Wieser, P. Mildner, & W. E. Holzinger (Eds.), *Rote Listen gefährdeter Tiere Kärntens* (pp. 99–104). Klagenfurt, Austria: Amt der Kärntner Landesregierung.

Hackländer, K., Ferrand, N., & Alves, P. C. (2008). Overview of Lagomorph research: What we have learned and what we still need to do. In P. C. Alves, N. Ferrand, & K. Hackländer (Eds.), *Lagomorph biology: Evolution, ecology, and conservation* (pp. 381–391). Berlin, Germany: Springer Verlag.

Hackländer, K., & Jenny, H. (2011). One man's meat is the other man's poison: How global warming affects *Lepus europaeus* and *Lepus timidus* in the Alps. *Mammalian Biology*, *76S*, 10.

Hanski, I. (1998). Metapopulation dynamics. *Nature*, *396*, 41–49.

Harrison, A. K. (2011). *Dispersal and compensatory population dynamics in a harvested mammal*. Dissertation University of Glasgow, Glasgow, 180 pp.

Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, *142*, 14–32.

Hewson, R. (1990). Behaviour, population changes and dispersal of mountain hares (*Lepus timidus*) in Scotland. *Journal of Zoology (London)*, *220*, 287–309.

Hiltunen, M., & Kauhala, K. (2006). Selection of sapling stand habitats by the mountain hare (*Lepus timidus*) during winter. *Mammalian Biology*, *71*, 183–189.

Hof, C., Levinsky, I., Araujo, M. B., & Rahbek, C. (2011). Rethinking species' ability to cope with rapid climate change. *Global Change Biology*, *17*, 2987–2990.

Hoffmann, A. A., & Sgro, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*, 479–485.

Hope, A. G., Waltari, E., Malaney, J. L., Payer, D. C., Cook, J. A., & Talbot, S. L. (2015). Arctic biodiversity: Increasing richness accompanies shrinking refugia for a cold-associated tundra fauna. *Ecosphere*, *6*, 159.

Hosmer, D. W., & Lemeshow, S. (2000). *Applied logistic regression* (2nd ed., p. 392). New York, Chichester, Weinheim, Brisbane, Singapore, Toronto: John Wiley & Son Inc..

Hughes, L. (2000). Biological consequences of global warming: Is the signal already apparent? *Trends in Ecology and Evolution*, *15*, 56–61.

Imperio, S., Bionda, R., Viterbi, R., & Provenzale, A. (2013). Climate change and human disturbance can lead to local extinction of Alpine rock ptarmigan: New insight from the Western Italian Alps. *PLoS One*, *8*, e81598.

IPCC (2014). *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, NY: Cambridge University Press.

Jackson, M. M., Gergel, S. E., & Martin, K. (2015). Effects of climate change on habitat availability and configuration for an endemic coastal alpine bird. *PLoS One*, *10*, e0142110.

Jansson, G., & Pehrson, A. (2007). The recent expansion of the brown hare (*Lepus europaeus*) in Sweden with possible implications to the mountain hare (*L. timidus*). *European Journal of Wildlife Research*, *53*, 125–130.

Kielland, K., Olson, K., & Euskirchen, E. (2010). Demography of snowshoe hares in relation to regional climate variability during a 10-year population cycle in interior Alaska. *Canadian Journal of Forest Research*, *40*, 1265–1272.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J. D., Schröder, B., Lindenborn, J., Reinfelder, V., ... Wilting, A. (2013). The importance of correcting for sampling bias in MAXENT species distribution models. *Diversity and Distributions*, *19*, 1366–1379.

Kutz, S. J., Hoberg, E. P., Polley, L., & Jenkins, E. J. (2005). Global warming is changing the dynamics of Arctic host-parasite systems. *Proceedings of the Royal Society B-Biological Sciences*, *272*, 2571–2576.

Leach, K., Kelly, R., Cameron, A., Montgomery, W. I., & Reid, N. (2015). Expertly validated models and phylogenetically-controlled analysis suggests responses to climate change are related to species traits in the order Lagomorpha. *PLoS One*, *10*, e0122267.

Lewis, C. W., Hodges, K. E., Koehler, G. M., & Mills, L. S. (2011). Influence of stand and landscape features on snowshoe hare abundance in fragmented forests. *Journal of Mammalogy*, *92*, 561–567.

Mace, G. M., & Purvis, A. (2008). Evolutionary biology and practical conservation: Bridging a widening gap. *Molecular Ecology*, *17*, 9–19.

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., ... Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, *12*, 1969–1976.

Mills, L. S., Zimova, M., Oyler, J., Running, S., Abatzoglou, J. T., & Lukacs, P. M. (2013). Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 7360–7365.

Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., & Beissinger, S. R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, *322*, 261–264.

Newey, S., & Thirgood, S. (2004). Parasite-mediated reduction in fecundity of mountain hares. *Proceedings of the Royal Society B-Biological Sciences*, *271*, S413–S415.

Newey, S., Thirgood, S., & Hudson, P. J. (2004). Do parasite burdens in spring influence condition and fecundity of female mountain hares *Lepus timidus*? *Wildlife Biology*, *10*, 171–176.

Nicol, A., Wiederholt, R., Diffendorfer, J. E., Mattsson, B. J., Thogmartin, W. E., Semmens, D. J. , ... Norris, D. R. (2016). A management-oriented framework for selecting metrics used to assess habitat- and path-specific quality in spatially structured populations. *Ecological Indicators*, *69*, 792–802.

Nodari, M. (2006). *Ecological role of mountain hare (*Lepus timidus*) in the alpine ecosystem. Habitat use, population consistency and dynamics of a species of conservation and management interest*. Dissertation University Insubria, Insubria, 134 pp.

Ott, E., Frehner, M., Frey, H. U., & Lüscher, P. (1997). *Gebirgsna-delwälder: Praxisorientierter Leitfaden für eine standortgerechte Wald-behandlung*. Bern, Switzerland; Stuttgart, Germany; Wien, Austria: Haupt Verlag.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, 37, 637–669.

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature, 421*, 37–42.

Pascual-Hortal, L., & Saura, S. (2006). Comparison and development of new graph-based landscape connectivity indices: Towards the priorization of habitat patches and corridors for conservation. *Landscape Ecology*, 21, 959–967.

Patthey, P., Signorell, N., Rotelli, L., & Arlettaz, R. (2012). Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: Conservation management implications. *European Journal of Wildlife Research*, 58, 59–70.

Pedersen, S., Odden, M., & Pedersen, C. (2017). Climate change induced molting mismatch? Mountain hare abundance reduced by duration of snow cover and predator abundance. *Ecosphere*, 8, e01722.

Pepin, N., Bradley, R. S., Diaz, H. F., Baraër, M., Caceres, E. B., Forsythe, N., ... Miller, J. R. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5, 424–430.

Pernollet, C. A., Körner-Nievergelt, F., & Jenni, L. (2015). Regional changes in the elevational distribution of the Alpine Rock Ptarmigan *Lagopus muta helvetica* in Switzerland. *Ibis*, 157, 823–836.

Phillips, S. J. (2016). *A brief tutorial on MAXENT, versions: 3.3.1*. Retrieved 12th December 2016, from www.cs.princeton.edu/~schapire/maxent/

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231–259.

Phillips, S. J., Dudik, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, 19, 181–197.

Porfirio, L. L., Harris, R. M. B., Lefroy, E. C., Hugh, S., Gould, S. F., Lee, G., ... Mackey, B. (2014). Improving the use of species distribution models in conservation planning and management under climate change. *PLoS One*, 9, e113749.

Raes, N., & Ter Steege, H. (2007). A null-model for significance testing of presence-only species distribution models. *Ecography*, 30, 727–736.

Reed, D. H., & Frankham, R. (2003). Correlation between fitness and genetic diversity. *Conservation Biology*, 17, 230–237.

Rehnus, M. (2013). *Der Schneehase in den Alpen. Ein Überlebenskünstler mit ungewisser Zukunft*. Bern, Switzerland; Stuttgart, Germany; Wien, Austria: Haupt Verlag.

Rehnus, M., & Bollmann, K. (2016). Non-invasive genetic population monitoring of mountain hares (*Lepus timidus*) in the Alps: Systematic or opportunistic sampling? *European Journal of Wildlife Research*, 62, 737–747.

Rehnus, M., Braunisch, V., Hackländer, K., Jost, L., & Bollmann, K. (2016). The seasonal trade-off between food and cover in the Alpine mountain hare (*Lepus timidus*). *European Journal of Wildlife Research*, 62, 11–21.

Rehnus, M., Marconi, L., Hackländer, K., & Filli, F. (2013). Seasonal changes in habitat use and feeding strategy of the mountain hare (*Lepus timidus*) in the Central Alps. *Hystrix*, 24, 161–165.

Rehnus, M., Palme, R., Filli, F., & Hackländer, K. (2010). Seasonal glucocorticoid secretion in mountain hares (*Lepus timidus*). *Mammalia*, 74, 347–350.

Rehnus, M., Wehrle, M., & Palme, R. (2014). Mountain hares *Lepus timidus* and tourism: Stress events and reactions. *Journal of Applied Ecology*, 51, 6–12.

Reid, N. (2011). European hare (*Lepus europaeus*) invasion ecology: Implication for the conservation of the endemic Irish hare (*Lepus timidus hibernicus*). *Biological Invasions*, 13, 559–569.

Riley, S. J., Degloria, S. D., & Elliot, R. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, 5, 23–26.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature (London)*, 421, 57–60.

Rudnick, D. A., Ryan, S. J., Beier, P., Cushman, S. A., Dieffenbach, F., Epps, C. W., ... Merenlender, A. M. (2012). The role of landscape connectivity inplanning and implementing conservation and restoration priorities. *Issues in Ecology*, 16, 1–20.

Saura, S., Estreguilb, C., Moutonb, C., & Rodríguez-Freireb, M. (2011). Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). *Ecological Indicators*, 11, 407–416.

Saura, S., & Pascual-Hortal, L. (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landscape and Urban Planning*, 83, 91–103.

Saura, S., & Torne, J. (2009). Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. *Environmental Modelling & Software*, 24, 135–139.

Schai-Braun, S., & Hackländer, K. (2016). Family Leporidae (Hares and rabbits). In D. E. Wilson, T. E. Lacher Jr, & R. A. Mittermeier (Eds.), *Handbook of the mammals of the world* (pp. 62–149). Barcelona, Spain: Lynx Edicions.

Schurr, F. M., Pagel, J., Cabral, J. S., Groeneveld, J., Bykova, O., O'Hara, R. B., ... Zimmermann, N. E. (2012). How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, 39, 2146–2162.

Schweiger, A. K., Nopp-Mayr, U., & Zohmann, M. (2012). Small-scale habitat use of black grouse (*Tetrao tetrix* L.) and rock ptarmigan (*Lagopus muta helvetica* Thienemann) in the Austrian Alps. *European Journal of Wildlife Research*, 58, 35–45.

Signorell, N., Wirthner, S., Patthey, P., Schranz, R., Rotelli, L., & Arlettaz, R. (2010). Concealment from predators drives foraging habitat selection in brood-rearing Alpine black grouse *Tetrao tetrix* hens: Habitat management implications. *Wildlife Biology*, 16, 249–257.

Slotta-Bachmayr, L. (1998). *Biologie und Ökologie des Alpenschneehasen (Lepus timidus varronis Miller 1901). Verbreitung, Raumnutzung, Aktivität und Habitatwahl in den Hohen Tauern*. Dissertation Paris London University Salzburg, Salzburg, 116 pp.

Sokolov, V. E., Ivanitskaya, E. Y., Gruzdev, V. V., & Heptner, V. G. (2009). *Lagomorphs, mammals of Russia and adjacent regions*. Washington, DC: Smithsonian Institution Libraries.

Speich, S., Abegg, M., Brändli, U.-B., Cioldi, F., Duc, P., Keller, M., ... Ulmer, U. (2011). *Drittes Schweizerisches Landesforstinventar – Ergebnistabellen im Internet. Zweite stark erweiterte Ausgabe*. Retrieved 19th June 2014, from www.lfi.ch/resultate

Stenkewitz, U., Nielsen, O. K., Skirnisson, K., & Stefansson, G. (2016). Host-Parasite interactions and population dynamics of Rock Ptarmigan. *PLoS One*, 11, e0165293.

The National Red List Project (2015). *The National Red List*. The National Red List project, London. Retrieved 12th August 2015, from www.nationalredlist.org

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148.

Thornton, P. E., Running, S. W., & White, M. A. (1997). Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology*, 190, 214–251.

Thuiller, W., Lavorel, S., & Araujo, M. B. (2005). Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, 14, 347–357.

Thulin, C. G. (2003). The distribution of mountain hares *Lepus timidus* in Europe: A challenge from brown hares *L. europaeus*? *Mammal Review*, *33*, 29–42.

Thulin, C.-G., & Flux, J. E. C. (2003). *Lepus timidus* Linnaeus, 1758 – Schneehase. In F. Krapp (Ed.), *Handbuch der Säugetiere Europas Band*, *3/II: Hasenartige Lagomorpha* (pp. 155–185). Wiebelsheim, Germany: Aula Publisher.

Van Der Wal, J., Shoo, L. P., Johnson, C. N., & Williams, S. E. (2009). Abundance and the environmental niche: Environmental suitability estimated from niche models predicts the upper limit of local abundance. *American Naturalist*, *174*, 282–291.

Van Strien, M. J., Keller, D., Holderegger, R., Ghazoul, J., Kienast, F., & Bolliger, J. (2014). Landscape genetics as a tool for conservation planning: Predicting the effects of landscape change on gene flow. *Ecological Applications*, *24*, 327–339.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., ... Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395.

Wilkening, J. L., Ray, C., Beever, E. A., & Brussard, P. F. (2011). Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. *Quaternary International*, *235*, 77–88.

Yandow, L. H., Chalfoun, A. D., & Doak, D. F. (2015). Climate tolerances and habitat requirements jointly shape the elevational distribution of the American Pika (*Ochotona princeps*), with implications for climate change effects. *PLoS One*, *10*, e0131082.

Yang, G. J. (1990). Physiological characteristics of pika *Ochotona rufescens rufescens* as a weak heat tolerant animal. *Tropical Medicine*, *32*, 129–140.

Zachos, F. E., Ben Slimen, H., Hackländer, K., Giacometti, M., & Suchentrunk, F. (2010). Regional genetic in situ differentiation despite phylogenetic heterogeneity in Alpine mountain hares. *Journal of Zoology*, *282*, 47–53.

Zimmermann, N. E., & Kienast, F. (1999). Predictive mapping of alpine grasslands in Switzerland: Species versus community approach. *Journal of Vegetation Science*, *10*, 469–482.

Zimova, M., Mills, L. S., & Nowak, J. J. (2016). High fitness costs of climate change-induced camouflage mismatch. *Ecology Letters*, *19*, 299–307.

SUPPORTING INFORMATION

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